View metadata, citation and similar papers at core.ac.uk

brought to you by CORE

provided by Elsevier - Publisher Connector

Vision Research 51 (2011) 898–907

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

# Saccadic updating of object orientation for grasping movements

L.P.J. Selen *, W.P. Medendorp

*Donders Institute for Brain, Cognition and Behaviour, Radboud University Nijmegen, The Netherlands*

ARTICLE INFO

*Article history:*
Received 9 September 2010
Received in revised form 29 December 2010
Available online 11 January 2011

*Keywords:*
Human
Reference frames
Spatial updating
Reach and grasp

ABSTRACT

Reach and grasp movements are a fundamental part of our daily interactions with the environment. This spatially-guided behavior is often directed to memorized objects because of intervening eye movements that caused them to disappear from sight. How does the brain store and maintain the spatial representations of objects for future reach and grasp movements? We had subjects ($n = 8$) make reach and two-digit grasp movements to memorized objects, briefly presented before an intervening saccade. Grasp errors, characterizing the spatial representation of object orientation, depended on current gaze position, with and without intervening saccade. This suggests that the orientation information of the object is coded and updated relative to gaze during intervening saccades, and that the grasp errors arose after the updating stage, during the later transformations involved in grasping. The pattern of reach errors also revealed a gaze-centered updating of object location, consistent with previous literature on updating of single-point targets. Furthermore, grasp and reach errors correlated strongly, but their relationship had a non-unity slope, which may suggest that the gaze-centered spatial updates were made in separate channels. Finally, the errors of the two digits were strongly correlated, supporting the notion that these were not controlled independently to form the grip in these experimental conditions. Taken together, our results suggest that the visuomotor system dynamically represents the short-term memory of location and orientation information for reach-and-grasp movements.

© 2011 Elsevier Ltd. All rights reserved.

## 1. Introduction

Many of our interactions with the world around us involve reaching for and grasping of objects. Even when we move, and objects in our surroundings disappear from sight, we can still keep track of them and act upon them whenever necessary. To achieve this spatial constancy in our motor behavior, it is thought that the brain updates and transforms spatial representations of objects within and across reference frames (Byrne, Cappadocia, & Crawford, 2010; Chang & Snyder, 2010; Crawford, Medendorp, & Marotta, 2004; McGuire & Sabes, 2009).

Recent behavioral studies suggest that the spatial update of object locations for goal-directed reaching movements takes place within a gaze-centered reference frame across intervening eye and body movements (e.g. Henriques, Klier, Smith, Lowy, & Crawford, 1998; Van Pelt & Medendorp, 2008). This gaze-centered updating behavior is consistent with observations in the medial parietal cortex showing the remapping of reach-related activity with changes of gaze, in both monkeys (Batista, Buneo, Snyder, & Andersen, 1999) and humans (Medendorp, Goltz, Vilis, & Crawford, 2003).

These updating experiments have typically been performed with subjects reaching or pointing to remembered single-point targets. In real life, however, reaching movements are often combined with a grasping movement. For such reach-and-grasp movements a multitude of object parameters needs to be defined. For example, to pick up the pen in front of you, not only information about its location is needed to transport the arm (transport component), but also knowledge about its size and orientation to shape the hand and fingers for an appropriate grasp (grip component). There is an abundance of studies that investigate the relation between object properties and grasping parameters (see Castiello, 2005 for review, Smeets & Brenner, 1999). However, to our knowledge, it is unknown in which reference frame orientation information of objects is encoded and maintained across eye movements and whether the update of object position and orientation takes place in a single or in distinct channels. This is the topic of the present study.

In the literature, it is argued that the spatial properties of an object – location and orientation – are processed by separate systems for reach-to-grasp actions (Arbib, 1981, Jeannerod, 1981, but see Smeets & Brenner, 1999), represented in distinct cortical modules. Neuropsychological studies, for example, have reported cases of patients who can reach accurately, but fail to grasp (Binkofski et al., 1998), as well as patients who make errors in reaching, but grasp appropriately (Cavina-Pratesi et al., 2010). Human

* Corresponding author. Address: Donders Institute for Brain, Cognition and Behaviour, P.O. Box 9104, 6500 HE, Nijmegen, The Netherlands. Fax: +31 24 361 6066.
*E-mail address:* l.selen@donders.ru.nl (L.P.J. Selen).

0042-6989/$ - see front matter © 2011 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2011.01.004

neuroimaging and monkey neurophysiological evidence suggests that neurons in medial parietal cortex (MIP) process the location of the object whereas those in the anterior intraparietal area (AIP) code the shape and orientation of the object for grasping (Cavina-Pratesi et al., 2010; Jeannerod, Arbib, Rizzolatti, & Sakata, 1995; Murata, Gallese, Luppino, Kaseda, & Sakata, 2000).

But even if there are separate spatial representations for the reach and grasp components of a movement, there should be a mechanism for combining them and subserving their coordinated action (Marotta, Medendorp, & Crawford, 2003). A common reference frame for the coding and updating of various spatial attributes of an object could facilitate a coordinated reach-and-grasp action. However, the existence of such a common reference frame has never been investigated.

Here, we used a reach-and-grasp task to test whether the associated spatial attributes of an object (location and orientation), briefly presented before an intervening saccade, are stored in a gaze-dependent or gaze-independent reference frame. Our test expands on a paradigm originally developed by Henriques et al. (1998) to examine the mechanism for location updating in reaching movements. Their paradigm exploits the fact that reaches with gaze directed to the target are fairly accurate and that reaches to targets that have only been presented in the periphery show clear error bias. The heart of the paradigm lies in the trials where a target is initially flashed on the fovea, but its remembered location shifted to the retinal periphery due to an intervening saccade. Henriques et al. (1998) found that reaches in this saccadic updating condition were similarly erred as reaches to gaze-peripheral targets, as if the bias arose after the reach target was updated relative to gaze, in the subsequent reference frame transformations for arm movement (see also Khan et al., 2005; Van Pelt & Medendorp, 2008).

Here we employed this paradigm to test how orientation information of objects is encoded and maintained across eye movements. Additionally we reasoned that if location constancy for reaching and orientation constancy for grasping employ the same reference frame, errors in orientation updating should correlate strongly with errors in location updating.

## 2. Methods

### 2.1. Subjects

Eight human participants (4 female, 4 male; mean age 21 ± 2 years), that were all naïve as to the purpose of the experiment, signed informed consent before participation. All reported to have no sensory, perceptual, or motor disorders. All participants used their preferred right arm to make reach-and-grasp movements.

### 2.2. Experimental setup

Subjects were seated in a completely darkened room, with their torso securely strapped into a custom-made chair by means of two safety belts across the torso and one across the pelvis to minimize body movement. Their head was mechanically stabilized using a chin rest and a helmet connected to the chair. This setup ensured that only the right arm and the eyes could move, while the head and torso remained stationary.

Reach-and-grasp movements were recorded in 3D with a sampling frequency of 125 Hz using an OPTOTRAK Certus motion tracking system (Northern Digital, Waterloo, Canada). Four infrared-emitting diodes (ireds) were positioned on the distal phalanx of both the thumb and index finger. Pointing measurements prior to the experiment defined the position of thumb- and finger tip relative to these ireds. Also the cornea position of the left and right eye was determined prior to the experiment. The actual center of the eye was assumed to be 1.3 cm behind the cornea. The position of the cyclopean eye (the mean location of the two eyes) served as the origin of the coordinate system. The $x$–$y$ plane was aligned perpendicular to gravity, with the positive $x$-axis rightward through the left and right eye, and the positive $y$-axis pointing forward.

Subjects' binocular eye movements were recorded at 250 Hz using an Eyelink II eyetracker (SR Research, Canada) mounted to the chair-fixed helmet. Eye movements were calibrated by fixating the stimulus LEDs, in complete darkness prior to the main experiment. This resulted in a calibration accuracy <0.5°. Calibration was updated offline, to allow for drift correction (see Van Pelt & Medendorp, 2008). Since the head and body stayed fixed during the experiment, the orientation of the eyes within the head, as measured by the tracker, was equivalent to the orientation of the eyes in space (gaze). Leftward rotations were taken as positive.

Two PCs in a master–slave arrangement controlled the experiment. The master PC contained hardware for data acquisition of the Optotrak measurements and visual stimulus control. The slave PC was equipped with hardware and software from the Eyelink system.

### 2.3. Stimuli

The stimulus array consisted of a frame with a rectangular target object (size 2.5 × 4.5 × 3.5 cm) in the center, and four fixation points indicated by LEDs, two on either side at a distance of 8.5 and 14.0 cm from the center of the target object, respectively. The positions of the target object and the stimulus targets were continuously tracked by the Optorak system. The target object was made of semi-transparent perspex and illuminated from the inside by a red LED-array. Also the fixation LEDs were red and had a luminance <20 mcd/m$^2$. The frame positions were controlled by a robotic arm, driven by stepping motors (type Animatics SmartMotors, Servo Systems). At the start of each trial the stimulus array was moved to one of three positions in the workspace. After stimulus presentation, the array was rapidly moved out of reach (<200 ms). The target block presented with its long axis in an orientation of 30° counterclockwise (seen from above) away from the $y$-axis. Target block and fixation points were presented at shoulder level in order to justify analysis of the data in the horizontal plane. Relative to the subject's cyclopean eye, the center of the target block was positioned at a distance of 40 cm from the cyclopean eye along the $y$-axis, and at eccentricities of −10°, 0°, or +10°. Within this configuration, the fixation LEDs adopted positions at −20°, −10°, 0°, 10°, and 20° directions from straight ahead.

### 2.4. Experimental paradigm

Fig. 1 illustrates the paradigm. Subjects were asked to reach and grasp for a remembered visual object that they had either foveated (control trials), had seen in the periphery while fixating an LED (fixation trials) or had first foveated and subsequently made a saccade to an LED (saccade trials). Trials were only started after the subjects had positioned their thumb and index finger onto a fixed starting block that was positioned 30 cm in front of the right shoulder. This ensured that all reaches started from the same posture. In control trials, subjects foveated the object for 1400 ms, after which the object was extinguished and removed from its original position. A beep instructed them to reach and grasp for the virtual object. In fixation trials, subjects were asked to grasp for the object after they had foveated an LED for 1400 ms, while the object was illuminated for the final 700 ms in the periphery. In saccade trials, subjects foveated the illuminated object for 700 ms, after which the object was extinguished and a saccade target LED was

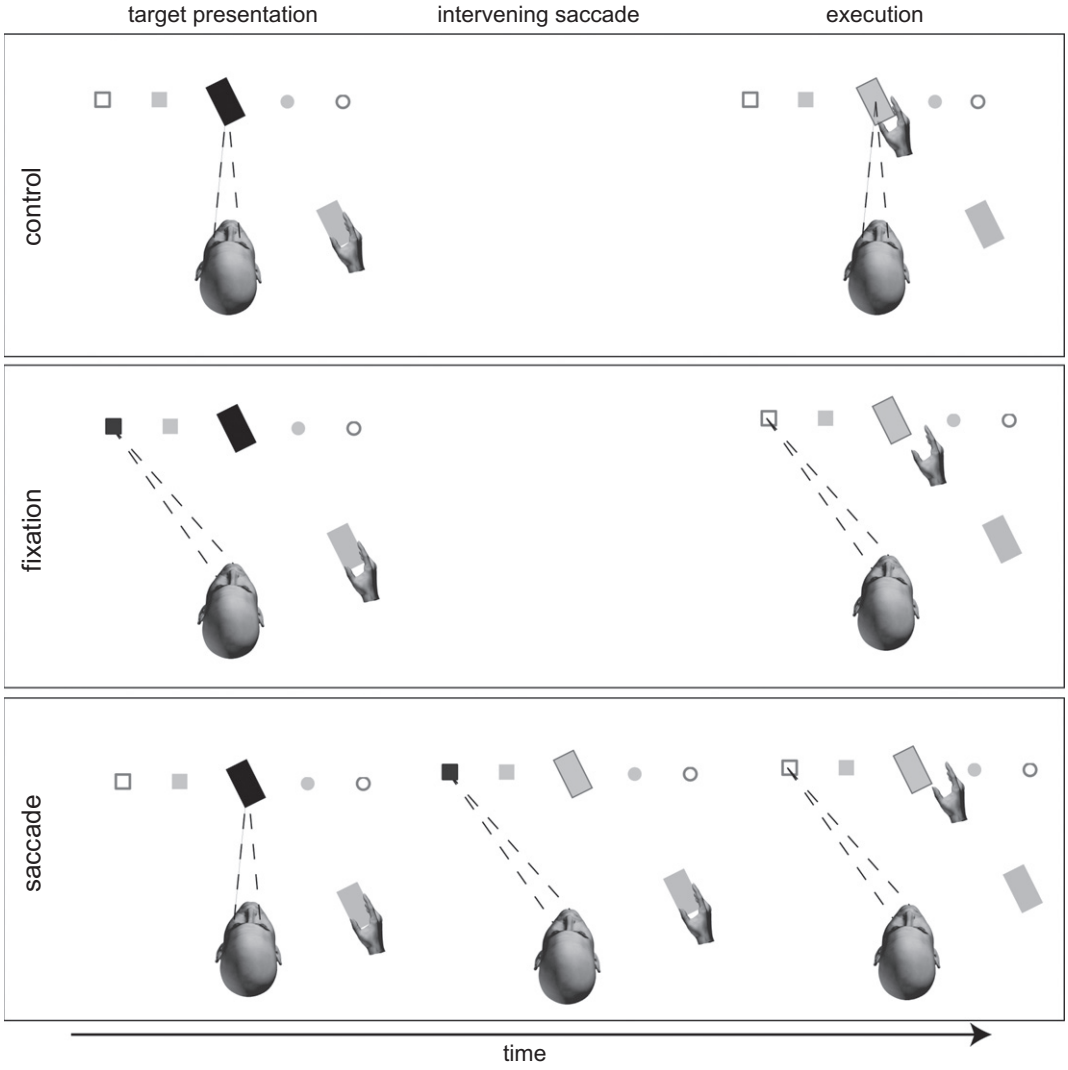


**Fig. 1.** Schematic of the experimental paradigm. In the control trials (first row), participants foveated the target object (black rectangle) while their hand was on the start object (gray rectangle). After the object had been extinguished and removed a beep was given and the subject was asked to grasp the, now virtual, object. In the fixation trials (second row), subjects foveated one of four LEDs (squares and circles) and the target object was presented in the periphery. Again, after removal of the object, subjects were asked to grasp for the object. In the saccade trials (third row), subjects first foveated the object and subsequently made a saccade to one out of four LEDs while the object was extinguished. Again subjects had to reach for the virtual object and grasp it between thumb and index finger. Note that the subject's head and hand are not to scale relative to the fixation LEDs and target object locations.

presented for 700 ms in the periphery. In all conditions, subjects were instructed to reach out quickly, accurately and as "naturally" as possible and as if they grasped the target block with a precision grip across its narrow width using thumb and index finger. Ten repetitions per condition were executed, making up a total of 270. Conditions were presented pseudo-randomly in blocks of 27 trials, containing all conditions once. The whole experiment took about an hour to be completed.

### 2.5. Data analysis

Data were analyzed off-line using Matlab (The Mathworks). We discarded trials in which subjects did not maintain fixation within a 1° interval around the fixation direction or made a saccade during target presentation. For the remaining trials, eye fixation accuracy was <1.0°. We also excluded trials in which subjects had not correctly followed the reaching instructions of the paradigm, i.e. when they started their reaching movement too early or did not adopt a stable reach position during the response intervals (fingertip velocity >0.5 cm/s based on Optotrak data). Overall, <7% of the trials was discarded on the basis of these arm and eye movement criteria. Movement trajectories were time normalized, averaged over the repetitions within a subject, and for plotting purposes, subsequently averaged across the subjects.

The end location and orientation of each movement was selected at the time at which the summed speed of distal phalanx of thumb and index finger reached its minimum and was below 0.5 cm/s.

The reach location was calculated as the average position of thumb and index finger at the reach endpoint. This measure of *reach endpoint* differs slightly from the commonly used wrist position to quantify the *transport part* of a reach-and-grasp movement. However, to characterize the spatial updating mechanisms it is more apt to examine the endpoint of the kinematic chain. The reach endpoint was converted into polar coordinates (reach angle and reach amplitude) relative to the cyclopean eye. A reach angle straight ahead of the cyclopean eye was defined as zero. The amplitude (depth) of the reaches was quantified as the length of the vector connecting the cyclopean eye and the reach location. Grasp orientation was quantified as the angle of the thumb to index finger vector relative to the coordinate axes system. In addition, we calculated the grip

aperture (GA, the distance between index finger and thumb) when the fingers reached their final location. Finally, the approach direction of the individual fingers was quantified as the movement direction in the 50 ms before the finger comes to a hold (inspired by Kleinholdermann, Brenner, Franz, and Smeets (2007)).

In a later stage of processing all reach directions, reach amplitudes, grasp orientations and finger approach directions were expressed relative to the control condition.

### 2.6. Geometric model of reach and grasp correlations

One of the key questions in this paper is whether updating of the reach location of an object and its grasp orientation are coupled mechanisms. Fig. 2 shows schematics of three possible dependencies between reach and grasp errors. Panel A shows arm configurations when reach errors are to the left and right of the true target location. In this case, the hand orientation, and thus grasp orientation, would be fixed relative to the forearm. The results are based on a simple geometric model of the arm (length upper arm: 32 cm and length forearm: 35 cm, cf. (Veeger, Yu, An, & Rozendal, 1997) that reaches to the same locations as observed in the experiment. This would be the case if no updating of grasp orientation takes place. The dashed line in panel B presents the predicted regression slope for reach and grasp errors, with the dots referring to the postures from panel A. Panel C shows an (extreme) example how grasp errors would change if the reach error was 45° and the grasp would be based on the same update as the reach, but now applied to all individual points of the object. The grasp orientation would rotate the same amount as the reach location and reach and grasp errors would be aligned along the identity axis (panel B, solid line). Clearly, the regression slope without grasp orientation updates (dashed line) is about 50% lower compared to the predicted slope when reach and grasp errors are caused by the same update (solid line). The final panel (D), shows that reach and grasp errors would be uncorrelated if reach errors were updated in a gaze-centered reference frame with polar coordinates axes and grasp orientation would be coded in a body-centered system with Cartesian coordinate axes. The dash-dotted line in panel B represents this updating scheme.

## 3. Results

Fig. 3A shows average reach-and-grasp trajectories averaged across subjects, for the two outer target blocks. To construct these trajectories all reaches were time normalized between movement onset and movement end before averaging. Beginning at the starting block, that standardized the initial posture of the hand and arm, the thumb and index finger were moved toward the remembered location of the target block. The solid gray traces show the thumb and index finger trajectories when the target block was foveated. On trials where the target block was seen in the left visual field reaches deviated to the left as well (black dashed traces). Similarly, reach-and-grasp movements deviated to the right if the subject viewed the object in the right visual field (black traces). Note that besides these directional errors, there were also errors in depth (amplitude errors).

Fig. 3B presents an example plot of the average end positions of thumb and index finger for the four different fixation points, for a single subject with fixation and saccade trials pooled together. When gaze is directed to the left of the target object, reach errors, i.e. the middle of the lines connecting thumb and index finger endpoint locations, are to the right and when gaze is directed to the right, reach errors are to the left. This result is in accordance with earlier observations when pointing with the index finger (Henriques et al., 1998). Also the grasp orientation, indicated by the line connecting thumb and index finger endpoints, shows systematic variations with gaze direction.

Fig. 4 presents the observed reach and grasp errors across all subjects, with the respective errors in the control trials serving as a baseline. Reach and grasp errors were not different for the three target block positions (ANOVA for reach errors: $F(2, 14) = 1.8$, $p = 0.20$ and for grasp errors: $F(2, 14) = 0.5$, $p = 0.606$) and for the remainder of the paper only the pooled data will be presented.

The top row of Fig. 4A–C shows the reach results and the bottom row (Fig. 4D–F) shows the grasp errors. When gaze is directed to the left of the target object, either continuously in a fixation trial (A and D) or temporarily in a saccade trial (B and E) reach errors are to the right and grasp errors are rotated clockwise relative (negative $y$-axis) to control. Likewise, when gaze is right of the target object, reach errors are to the left and grasp errors rotate counterclockwise (positive $y$-axis). To unravel the reference frame that underlies updating of object position and orientation in saccade trials, we contrast them with the behavior observed in the control and fixation trials. If updates of target position and orientation across saccades take place in a gaze-dependent reference frame, one would expect the errors observed in the fixation trials to be the same as in the saccade trials, since the location and

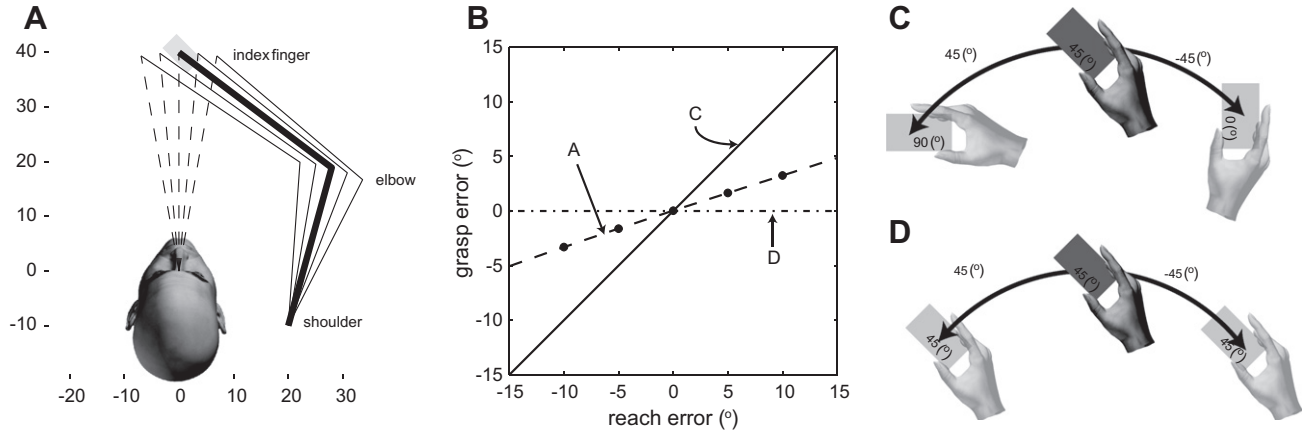


**Fig. 2.** Theoretical reach and grasp error relations for three updating schemes. (A) Gaze-centered updating of reach locations and no updating of grasp orientation. The hand, and thus grasp, orientation is fully determined by the orientation of the forearm. (C) Gaze-centered updating of both reach and grasp errors with errors arising from the same updating module. In this case the grasp orientation rotates one-to-one with the reach direction in a polar coordinate system attached to the cyclopean eye. (D) Gaze-centered updating of the reach location and constancy of the grasp orientation in Cartesian coordinates. (B) Dashed line shows how reach and grasp errors would be correlated if the hand orientation remained constant relative to the forearm. Solid line represents theoretical correlation between reach and grasp errors if they both stem from the same mechanism. If grasp orientation is updated in Cartesian coordinates and reach in gaze-centered coordinates, the error pattern should follow the dash-dotted line.

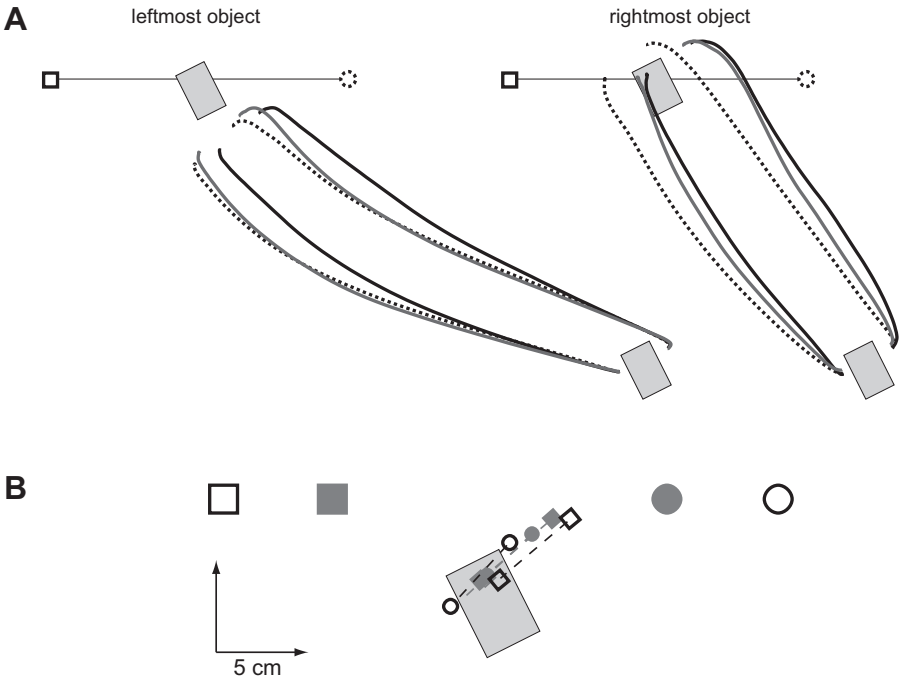


**Fig. 3.** (A) Average reach-and-grasp trajectories across subjects for the leftmost and rightmost object position. Solid and dashed black lines represent reaches when the eyes are oriented to the outer left and outer right fixation point respectively. Solid gray line is for the control reaches when fixation is on the target block. Figure is to scale. (B) Average reach positions and grasp orientations for the four gaze directions. Data from fixation and saccade trials have been merged. When gaze is directed to the left of the target block, reach errors are to the right and vice versa. Similarly, the grasp orientation changes systematically with gaze direction. The four gaze-directions are indicated by squares and circles and the corresponding grasp endpoint by the same symbols connected by a line.

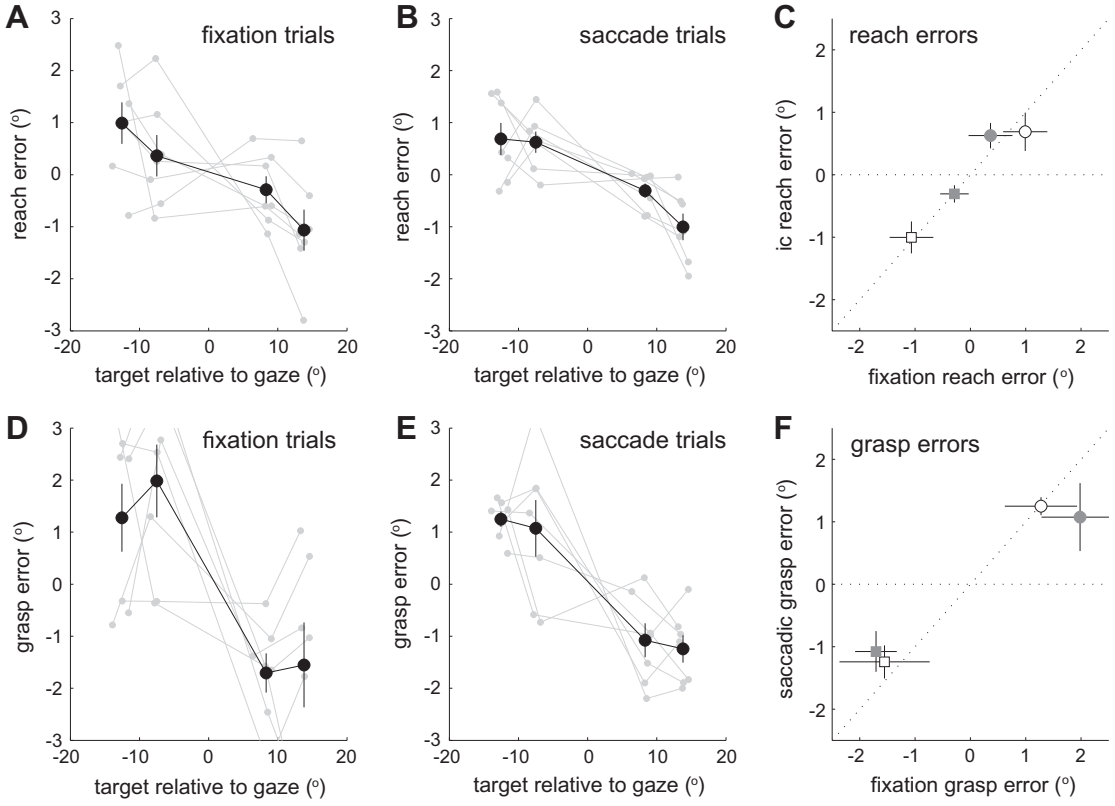


**Fig. 4.** Systematic errors for reaches and grasps in fixation and saccade trials as a function of target location relative to gaze. Plots show the mean and standard error of the mean across subjects. Data are pooled across the three object positions and normalized to the observed reach and grasp errors in control trials where subjects foveated the target object before reaching and grasping for the object. (A and D) The errors in the fixation trials for reach and grasp errors respectively. (B and E) The same errors for the saccade trials. (C) Shows how reach errors in fixation and saccade trials are correlated and (F) shows the same for grasp errors. The same symbols (open and closed squares and circles) as in Figs. 1 and 3 are used to indicate the corresponding gaze-directions.

orientation are the same relative to gaze in both trial types. On the other hand, if the update is gaze-independent, the errors in the saccade trials should be uncorrelated to the errors in the fixation trials, but similar to the control trials, because now only the gaze direction when observing the object matters. Thus, the crucial step to show that reach locations and grasp orientations are updated in a gaze-dependent reference is to show that errors observed in fixation and saccade trials are the same (Henriques et al., 1998).

Fig. 4C shows that reach errors for fixation and saccade trials are indeed identical, as confirmed by repeated-measures ANOVA ($F(1, 7) = 1.42$; $p > 0.27$). Similarly, Fig. 4F shows that grasp errors were indistinguishable between fixation and saccade trials, as confirmed by repeated-measures ANOVA ($F(1, 7) = 0.04$; $p > 0.84$). To reaffirm, we also looked at the regression slope between fixation and saccade trials for both reach and grasp errors. The $R^2$ values for the regression were 0.42 for the reach errors and 0.49 for the grasp errors. The slopes of the regression between reach errors in fixation and saccade trials were not different from one ($t(7) = 0.96$; $p = 0.37$). Also, the slope for the regression of grasp errors was not different from one ($t(7) = -1.26$; $p = 0.25$).

The systematic errors in fixation and saccade trials are thus statistically indistinguishable, suggesting that the update of both target object location and orientation across eye-movements takes place in a gaze-centered representation. Further support for this conclusion comes also from inspection of the variability of the data. As Fig. 4 shows, the error pattern for both grasping and reaching is less variable in the saccade than fixation trials, also within individual subjects. The likely reason is that in the saccade conditions, movements are based on a remapped but precise, foveally-derived spatial representation while in the fixation condition a less precise, extrafoveally-derived representation guides the movement (Schlicht & Schrater, 2007; Vaziri, Diedrichsen, & Shadmehr, 2006).

Do the location updates and orientation updates have the same gain? To study the coupling between reach and grasp errors, we compared them on a trial-by-trial basis, since we have paired samples of them. If errors in reach and grasp movements stem from the same neuronal updating process, they should be correlated. Fig. 5A shows reach versus grasp errors for an exemplar subject. Each symbol represents a trial, with fixation and saccade trials mixed together. The three different symbols represent the three object positions. Both reach and grasp errors were normalized to the reach- and grasp angles in the control trials. The solid line is the regression to the pooled data across all object positions. Regression slopes for the three object positions were indistinguishable. Similarly, Fig. 5B shows the regression lines for the individual subjects; all regressions were significant ($p < 0.001$). The dashed line shows the predicted correlation when hand orientation maintained fixed relative to the forearm (see Fig. 2 and Section 2). Clearly, the slopes from the experimental data are steeper for all subjects and therefore our result is not simply an effect of limb biomechanics. The regression slopes range from 1.6 to 5.1, with correlation coefficients spanning the range from 0.15 to 0.64, indicating that also the perfect coupling hypothesis of reach and grasp updates (solid gray line) does not hold.

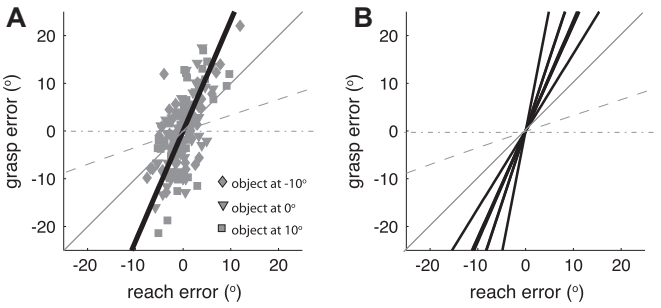


**Fig. 5.** Correlations of reach and grasp errors. (A) Reach and grasp errors in a single subject for the three object positions. The black line shows the regression line across all object positions, since object positions were indistinguishable based on the errors. (B) The regression lines for all individual subjects, again pooled across object positions. In both panels the gray lines indicate the predictions from the updating schemes presented in the methods: The dashed line represents the correlation as predicted from the model where orientation is not updated across gaze-shifts and is fixed with respect to the forearm. The dash-dotted line shows the prediction of orientation updating is gaze independent and the solid gray line is the identity axis, referring to location and orientation updating being perfectly coupled.

To further analyze the grasp and reach errors, we examined the differences in grip aperture and the amplitude (i.e. depth) of the reaches across conditions. As shown in Fig. 6, grip aperture increases for objects at more eccentric locations relative to gaze (panels A and B; $F(3, 21) = 5.66$, $p = 0.005$). This in itself is already an indication that updates take place in a gaze-centered reference frame. That is, grip aperture increases because the (visual) uncertainty of target location and orientation increases when viewed, or updated to more peripheral locations (Schlicht & Schrater, 2007). Aperture errors in fixation trials and saccade trials showed no systematic differences ($F(1, 7) = 3.94$, $p = 0.08$). Likewise, regression slopes of the errors in the fixation versus saccade trials could statistically not be distinguished from one ($t(7) = -0.24$; $p = 0.82$; $R^2 = 0.35$; Fig. 6C).

Also for amplitude, we found no significant difference between the errors in fixation and saccade trials ($F(1, 7) = 0.86$, $p = 0.38$, Fig. 6D–F). However, this lack of significance was attributable to an interaction between fixation eccentricity and condition $F(3, 21) = 5.31$, $p = 0.006$), which resulted in a slope that was significantly different from one ($t(7) = -2.58$; $p = 0.04$; $R^2 = 0.35$).

Finally, we performed an analysis at the level of the two individual digits to test the hypothesis the grasp and reach errors depend on gaze-dependent position and update of the left (for the thumb position) and right (for index finger position) block edge, separately. In this case, based on previous literature (Henriques et al., 1998), it could be expected that if gaze is directed left of the target block its right edge is more peripheral in gaze-coordinates than its left edge resulting in a different target approach direction of the index finger compared to the thumb and vice versa.

To test this, we examined the approach direction of each digit during the final 50 ms of the movement, thus when the digits get close to the imagined surface of the object (see Kleinholdermann et al. (2007) for more detail of this approach). Fig. 7 shows, for both thumb (upper panels) and index finger (lower panel), a systematic relationship between their approach direction (relative to control trials) and gaze direction, in both fixation and saccade trials. A repeated-measures ANOVA did not reveal significant differences between the errors in the two trial types ($F(1, 7) = 0.88$; $p = 0.38$), supporting the gaze-centered updating hypothesis.

To complete our analysis, we compared the errors in approach direction (relative to the control) of the two digits, pooling across all trial types. Fig. 8 shows a highly significant correlation ($r > 0.84$, $p < 0.001$) for the individual subjects. This strong coupling suggests that the index finger and thumb did not move independently to positions to form the grip, at least in these experimental conditions.

## 4. Discussion

Spatial updating is the process by which we keep track of objects in the space around us, even as we move. Most studies to date have addressed the question of how we update the locations of single-point objects. This has led to the hypothesis that locations are coded in gaze-centered coordinates, which are adjusted in

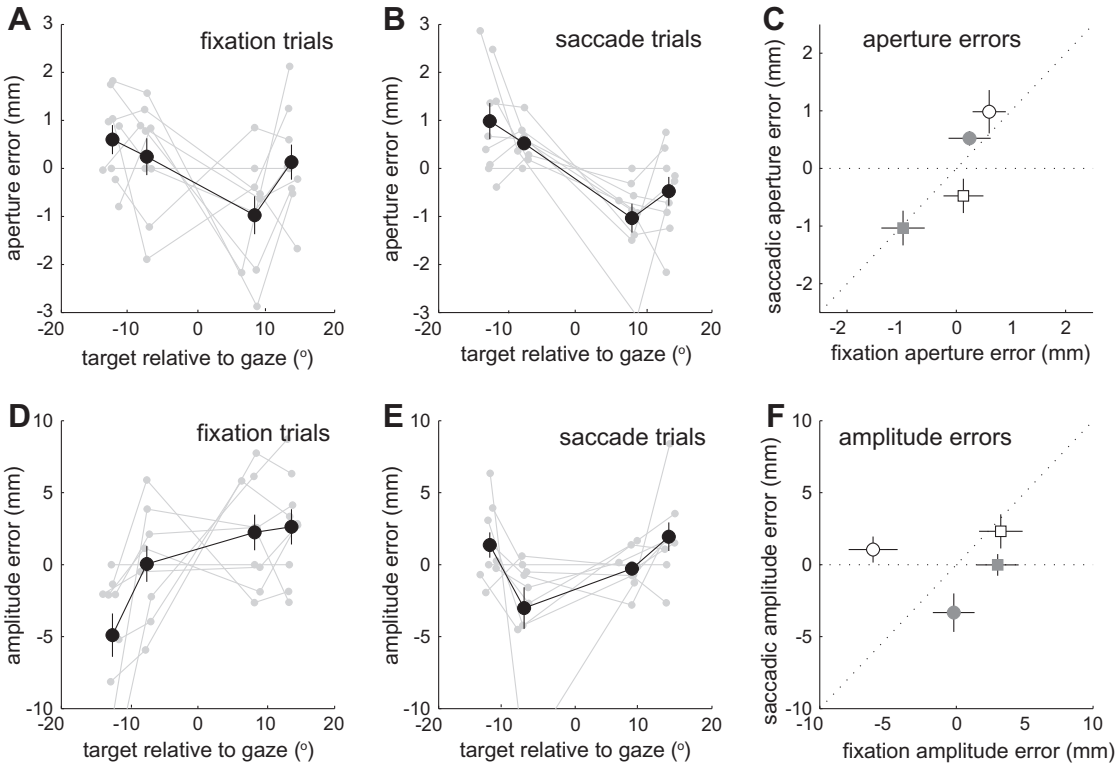


**Fig. 6.** Systematic errors for final grip aperture and reach amplitude in fixation and saccade trials as a function of target location relative to gaze. See caption of Fig. 4 for further details.

conjunction with eye movements. In the present study, we tested the mechanisms underlying the representation and update of object location *and* orientation, by measuring the errors in reach-and-grasp movements to remembered objects, seen prior to an intervening saccade.

Our main findings are the following: (i) the reach errors demonstrated gaze-centered updating, consistent with previous studies on reaching or pointing to single-point targets, (ii) the grasp errors also demonstrated gaze-centered coding and updating of object orientation, (iii) the grasp errors strongly correlated with the reach errors, but with non-unity gain, suggesting that object orientation and locations are updated by a common mechanism, but likely in separate computational modules. (iv) The errors of the two individual digits demonstrated a high correlation, indicating they were not controlled independently to form the grip in these updating conditions. These findings will now be discussed in more detail.

Previous studies showing gaze-dependent updating of space have used simple acts to single-point targets. More specifically, these studies used saccade-and-point movements to show the coding and updating of the spatial direction (i.e. one dimension of location) of the target. Following up on the first observations by Henriques et al. (1998), such gaze-centered direction updates were also observed for auditory and proprioceptive pointing targets (Fiehler, Rosler, & Henriques, 2010; Jones & Henriques, 2010; Pouget, Ducom, Torri, & Bavelier, 2002), for targets at different distances (Medendorp & Crawford, 2002; Van Pelt & Medendorp, 2008) and for targets inferred from motion patterns (Poljac & van den Berg, 2003). Here we add to these findings that even locations of objects that need to be acted upon by more complex actions, requiring coordinated limb, hand and finger movements, are coded and spatially-updated in egocentric, gaze-dependent coordinates.

The object's orientation, as well as its size, dictates how to form the hand and fingers appropriately for the grasp. Thus, on each occasion that a grasping movement must be made, the egocentric coordinates of the object's orientation must be computed. At this level of movement generation, the particular coordinate system must be effector-dependent; however, at an earlier stage – for pending actions – the brain may use a higher-level sensory-based reference frame to store the object's structure (Andersen & Buneo, 2002). Here we show for the first time that, like the representation of location information, the short-term memory of the orientation of the object is also coded in vision-based, gaze-centered coordinates, and updated across eye movement.

In close connection, Schlicht and Schrater (2007) investigated the effect of object location uncertainty, manipulated by changing gaze direction relative to object location, on the maximum grip aperture and argue for a gaze-centered storage of object location. Our aperture results are in line with their observations, although they did not explicitly look at orientation updates. The fact that we find systematic effects of target eccentricity on grip aperture, suggests that our brain takes uncertainty into account, even in a pantomimed task as used here.

We do not want to make strong claims in terms of the long-standing debate of whether, at the execution stage, the digits move relative to each other to form the grip or whether they move independently to positions on the object (Smeets & Brenner, 1999). In our experimental conditions, we did find a strong correlation between the approach directions of the two digits, when they come near the target object. If these results could be generalized to the execution level, they suggest the two digits were not controlled independently to form the grip, but this would require further validation perhaps by using different target shapes (Kleinholdermann et al., 2007). Although separating transport and grip or separating between individual digit movements are both viable theoretical leanings, the former is argued to be simpler from a control perspective (Oztop & Kawato, 2009). Learning of a single controller for each digit might be difficult; dealing with smaller and simpler controllers (i.e. for the hand and the arm) and coordinating them according to the task requirements has been argued more plausible (Kawato & Samejima, 2007).

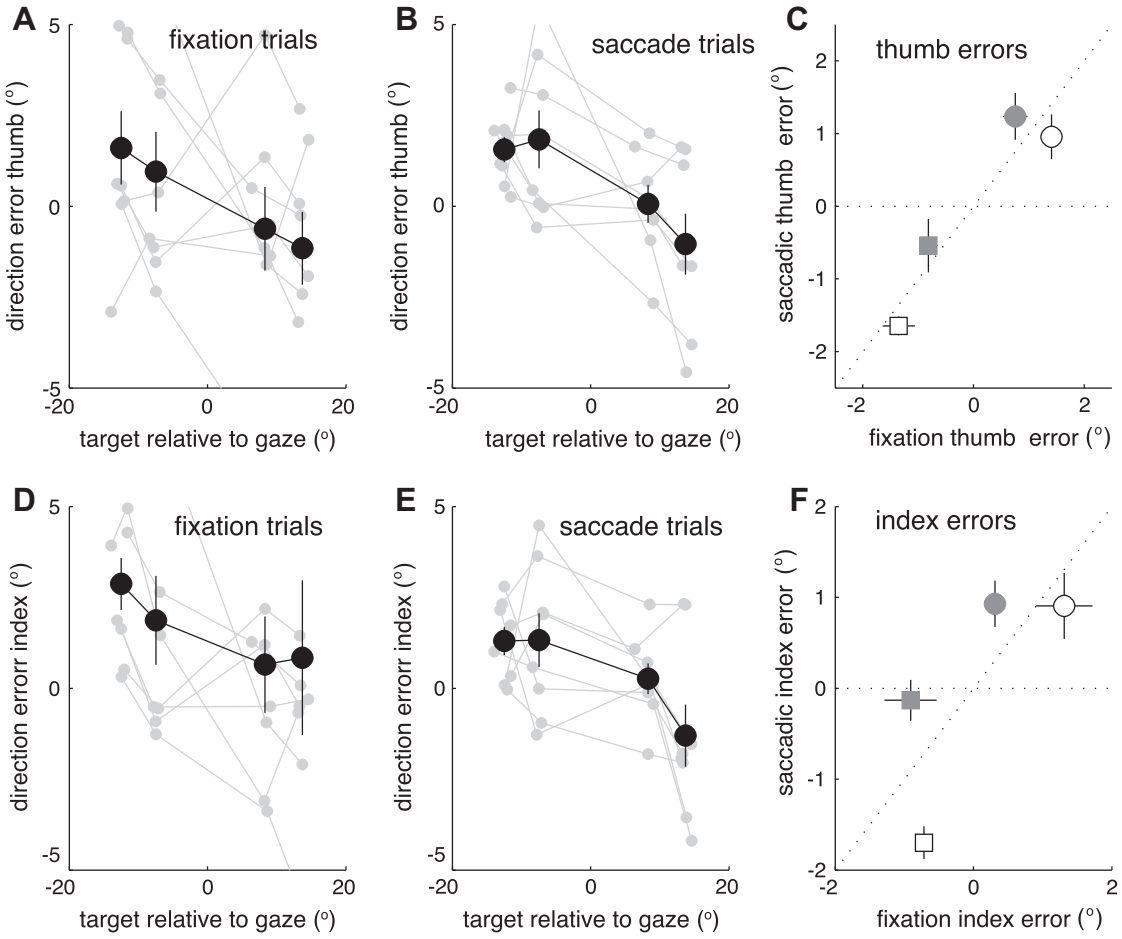


**Fig. 7.** Systematic errors of the thumb and in fixation and saccade trials as a function of target location relative to gaze. Errors are computed as direction of the final 50 ms of the movement of each digit, when the two digits are closely approaching the imagined surface of the target. See caption of Fig. 4 for further details.

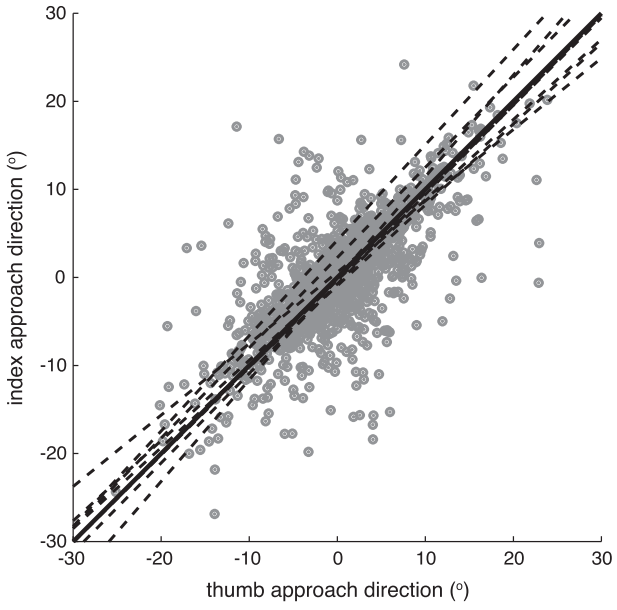


**Fig. 8.** Scatterplots of errors in the movements of the index finger and thumb. Each data point represents a single trial. Data pooled across conditions and subjects (dots). Major axis regression fits for the individual subject (dashed lines) and the identity axis (solid line) are plotted on top.

It should be realized that the systematic reach and grasp errors we found and exploited here do not likely reflect a gaze-centered bias in the representation. Our results show that they depend on current eye position, irrespective of whether an intervening saccade occurred. This suggests that the object properties are recomputed after the saccade, and therefore that the grasp and reach errors arise after this gaze-centered updating stage, in the respective visuomotor transformations (Khan et al., 2005; Van Pelt & Medendorp, 2008).

Furthermore, it has been argued that pantomimed reaches use different neural pathways than natural reaches (Goodale, Jakobson, & Keillor, 1994; Westwood, Chapman, & Roy, 2000), with pantomimed actions being mediated by the ventral stream and natural actions by the dorsal stream. In this view, our pantomimed actions would tap into the ventral stream, looking at the perceptual storage of object location and orientation. However, here we used pantomimed actions to examine the mechanisms of spatial updating, as in previous literature. How much this involves the ventral stream cannot be inferred from our results; the observation of an egocentric, gaze-centered nature of the updating mechanism points certainly to a role of the dorsal stream. That said, the present results do not exclude the possibility that spatial object information is coded in multiple reference frames (Beurze, Toni, Pisella, & Medendorp, 2010; Byrne et al., 2010; McGuire & Sabes, 2009). Here we have probed the gaze-centered updating mechanism, but we do not want to claim that it is the only mechanism. For example one could argue that part of our result can be explained by a shoulder centered reference frame, which could change the slope of reach vs. grasp errors.

Nevertheless, our results argue in favor of a common gaze-centered mechanism in the coding of orientation and location

information. The fact that the grasp and reach errors correlate so strongly (see Fig. 6), even in individual subjects, is further support for this notion. We have ruled out the possibility that this relationship is only caused by biomechanical constraints without any updating of object orientation taking place. A heuristic model of the arm that did not update its 'grasp orientation', revealed a slope of ~0.3 (Figs. 2B and 6A) between object azimuth relative to the *cyclopean eye* and grasp orientation. Experimental limits on the biomechanical contributions can be derived from Schot, Brenner, and Smeets (2010), who found a slope of 1.06 between object azimuth with respect to the *shoulder* and grip orientation when subjects' grasp orientation was unconstrained while grasping for cylinders. Conversion of their results to the cyclopean eye resulted in a slope of ~0.6, which is also significantly lower than the observed values that were all above one (Fig. 6B).

The correlation between reach and grasp errors by itself cannot simply be taken to imply that the processing of location and information is performed by one and the same module. In that case, location and orientation updates should have revealed a one-to-one relationship between the reach and grasp errors. In fact, closer consideration of this relationship may hint at the idea of separate channels in the processing this information. The slope of the relationship is clearly larger than one, suggesting that each component is updated in parallel, with its own updating gain (Soechting & Flanders, 1993). While our results suggest the parallel updating of location and orientation information, the high correlation between the grasp and reach errors clearly indicates that there is some coupling between the two streams, perhaps related to degree of on-line control required by the prehension movement (Grol et al., 2007).

Considering our updating results at the neural level, they speak to the proposed distinction between dorsomedial "reaching" versus dorsolateral "grasping" substreams in the human parietal-frontal circuit dedicated to spatial coding for reach-and-grasp actions (Cavina-Pratesi et al., 2010). The dorsalmedial stream, which includes areas V6a and MIP (together termed the parietal reach region, PRR) and the dorsal premotor cortex (PMd) is responsive to reach movements. PRR's selectivity for target locations is better described in gaze-centered coordinates than in shoulder-centered coordinates. Furthermore activity in PPR is updated with changes in gaze (Batista et al., 1999; Medendorp et al., 2003). PMd neurons show a relative-position code for target, gaze, and hand position (Pesaran, Nelson, & Andersen, 2006). In this regard, the observed reach errors, reflecting gaze-centered updating of target location, are consistent with the physiology in this processing stream.

The dorsolateral stream, including areas AIP and PMv, processes the intrinsic properties of objects for the purpose of manipulation. Of the two regions, AIP has been suggested to code in visual terms, specifically for precision grips, while PMv operates at the motor level (see Castiello, 2005, for review). To our knowledge, the spatial reference frame of neurons in AIP has not been studied, let alone that the behavior of neurons is tested in updating conditions. Based on the present results, we propose that the physiological implementation of the coding and updating of object orientation for grasp in AIP takes place in a gaze-centered reference frame.

In conclusion, our results suggest that the brain dynamically represents the short-term memory of location and orientation information for reach-and-grasp movements, perhaps by using distinct channels that both operate and update their information in a gaze-centered reference frame.

## Acknowledgments

This research was supported by The Netherlands Organization for Scientific Research (Grant No. 400-07-003). We thank Malte Koester for his help during the data analysis.

## References

Andersen, R. A., & Buneo, C. A. (2002). Intentional maps in posterior parietal cortex. *Annual Review of Neuroscience, 25*, 189–220.

Arbib, M. A. (1981). Perceptual structures and distributed motor control. In V. B. Brooks (Ed.), *Handbook of physiology – The nervous system II. Motor control* (pp. 1449–1480). American Physiological Society.

Batista, A. P., Buneo, C. A., Snyder, L. H., & Andersen, R. A. (1999). Reach plans in eye-centered coordinates. *Science, 285*(5425), 257–260.

Beurze, S. M., Toni, I., Pisella, L., & Medendorp, W. P. (2010). Reference frames for reach planning in human parietofrontal cortex. *Journal of Neurophysiology, 104*(3), 1736–1745.

Binkofski, F., Dohle, C., Posse, S., Stephan, K. M., Hefter, H., Seitz, R. J., et al. (1998). Human anterior intraparietal area subserves prehension: A combined lesion and functional MRI activation study. *Neurology, 50*(5), 1253–1259.

Byrne, P. A., Cappadocia, D. C., & Crawford, J. D. (2010). Interactions between gaze-centered and allocentric representations of reach target location in the presence of spatial updating. *Vision Research, 50*(24), 2662–2670.

Castiello, U. (2005). The neuroscience of grasping. *Nature Reviews Neuroscience, 6*(9), 726–736.

Cavina-Pratesi, C., Monaco, S., Fattori, P., Galletti, C., McAdam, T. D., Quinlan, D. J., et al. (2010). Functional magnetic resonance imaging reveals the neural substrates of arm transport and grip formation in reach-to-grasp actions in humans. *Journal of Neuroscience, 30*(31), 10306–10323.

Chang, S. W. C., & Snyder, L. H. (2010). Idiosyncratic and systematic aspects of spatial representations in the macaque parietal cortex. *Proceedings of the National Academy of Sciences of the United States of America, 107*(17), 7951–7956.

Crawford, J. D., Medendorp, W. P., & Marotta, J. J. (2004). Spatial transformations for eye–hand coordination. *Journal of Neurophysiology, 92*(1), 10–19.

Fiehler, K., Rosler, F., & Henriques, D. Y. (2010). Interaction between gaze and visual and proprioceptive position judgements. *Experimental Brain Research, 203*(3), 485–498.

Goodale, M. A., Jakobson, L. S., & Keillor, J. M. (1994). Differences in the visual control of pantomimed and natural grasping movements. *Neuropsychologia, 32*(10), 1159–1178.

Grol, M. J., Majdandzic, J., Stephan, K. E., Verhagen, L., Dijkerman, H. C., Bekkering, H., et al. (2007). Parieto-frontal connectivity during visually guided grasping. *Journal of Neuroscience, 27*(44), 11877–11887.

Henriques, D. Y., Klier, E. M., Smith, M. A., Lowy, D., & Crawford, J. D. (1998). Gaze-centered remapping of remembered visual space in an open-loop pointing task. *Journal of Neuroscience, 18*(4), 1583–1594.

Jeannerod, M. (1981). Specialized channels for cognitive responses. *Cognition, 10*(1–3), 135–137.

Jeannerod, M., Arbib, M. A., Rizzolatti, G., & Sakata, H. (1995). Grasping objects: The cortical mechanisms of visuomotor transformation. *Trends in Neurosciences, 18*(7), 314–320.

Jones, S. A., & Henriques, D. Y. (2010). Memory for proprioceptive and multisensory targets is partially coded relative to gaze. *Neuropsychologia*.

Kawato, M., & Samejima, K. (2007). Efficient reinforcement learning: Computational theories, neuroscience and robotics. *Current Opinion in Neurobiology, 17*(2), 205–212.

Khan, A. Z., Pisella, L., Vighetto, A., Cotton, F., Luaute, J., Boisson, D., et al. (2005). Optic ataxia errors depend on remapped, not viewed, target location. *Nature Neuroscience, 8*(4), 418–420.

Kleinholdermann, U., Brenner, E., Franz, V. H., & Smeets, J. B. (2007). Grasping trapezoidal objects. *Experimental Brain Research, 180*(3), 415–420.

Marotta, J. J., Medendorp, W. P., & Crawford, J. D. (2003). Kinematic rules for upper and lower arm contributions to grasp orientation. *Journal of Neurophysiology, 90*(6), 3816–3827.

McGuire, L. M., & Sabes, P. N. (2009). Sensory transformations and the use of multiple reference frames for reach planning. *Nature Neuroscience, 12*(8), 1056–1061.

Medendorp, W. P., & Crawford, J. D. (2002). Visuospatial updating of reaching targets in near and far space. *Neuroreport, 13*(5), 633–636.

Medendorp, W. P., Goltz, H. C., Vilis, T., & Crawford, J. D. (2003). Gaze-centered updating of visual space in human parietal cortex. *Journal of Neuroscience, 23*(15), 6209–6214.

Murata, A., Gallese, V., Luppino, G., Kaseda, M., & Sakata, H. (2000). Selectivity for the shape, size, and orientation of objects for grasping in neurons of monkey parietal area AIP. *Journal of Neurophysiology, 83*(5), 2580–2601.

Oztop, E., & Kawato, M. (2009). The control of grasping. In D. Nowak & J. Hermsdorfer (Eds.), *Sensorimotor control of grasping: Physiology and pathophysiology*. Cambridge University Press.

Pesaran, B., Nelson, M. J., & Andersen, R. A. (2006). Dorsal premotor neurons encode the relative position of the hand, eye, and goal during reach planning. *Neuron, 51*(1), 125–134.

Poljac, E., & van den Berg, A. V. (2003). Representation of heading direction in far and near head space. *Experimental Brain Research, 151*(4), 501–513.

Pouget, A., Ducom, J. C., Torri, J., & Bavelier, D. (2002). Multisensory spatial representations in eye-centered coordinates for reaching. *Cognition, 83*(1), B1–B11.

Schlicht, E. J., & Schrater, P. R. (2007). Impact of coordinate transformation uncertainty on human sensorimotor control. *Journal of Neurophysiology, 97*(6), 4203–4214.

Schot, W. D., Brenner, E., & Smeets, J. B. (2010). Posture of the arm when grasping spheres to place them elsewhere. *Experimental Brain Research, 204*(2), 163–171.

Smeets, J. B., & Brenner, E. (1999). A new view on grasping. *Motor Control, 3*(3), 237–271.

Soechting, J. F., & Flanders, M. (1993). Parallel, interdependent channels for location and orientation in sensorimotor transformations for reaching and grasping. *Journal of Neurophysiology, 70*(3), 1137–1150.

Van Pelt, S., & Medendorp, W. P. (2008). Updating target distance across eye movements in depth. *Journal of Neurophysiology, 99*(5), 2281–2290.

Vaziri, S., Diedrichsen, J., & Shadmehr, R. (2006). Why does the brain predict sensory consequences of oculomotor commands? Optimal integration of the predicted and the actual sensory feedback. *Journal of Neuroscience, 26*(16), 4188–4197.

Veeger, H. E., Yu, B., An, K. N., & Rozendal, R. H. (1997). Parameters for modeling the upper extremity. *Journal of Biomechanics, 30*(6), 647–652.

Westwood, D. A., Chapman, C. D., & Roy, E. A. (2000). Pantomimed actions may be controlled by the ventral visual stream. *Experimental Brain Research, 130*(4), 545–548.